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Plebejus argus (L) caernensis Thompson. A Stenoecious Geotype

By R. L. H. Dennis

In a recent work on *Eumenis semele thyone* Th., the writer pointed out the remarkable parallelism of the distributional and morpho-reductionalist criteria connecting this sub-species with *P. argus caernensis* Th. He explained that any historical reconstruction of their origin must take into account the nature of both subspecies, and that certain points were foremost in any discussion:—

(i) The remarkable sympatric distribution on the west side of the Gt. Orme of two totally unrelated sub-species.

(ii) The certified parallelism in their genetic endowment such as the early emergence and dwarfed nature of both subspecies.

(iii) The final facet, though not perhaps as remarkable as previous authors have held it to be, is the unusual environment of *P. argus* on limestone slopes, and its adopted foodplant— Helianthemum nummularium.

This paper is not intended as an all inclusive work on the subject of this race, but provides a stop-gap covering two aspects of some importance. The first is a brief account of the distributional and morpho-criteria of the race, pointing out some of the changes that have occurred with time in the colonies; and dealing with aspects of *caernensis* that would reflect upon conclusions concerning the origins of both races dealt with in an earlier account on *E. semele thyone* Th. These form topic headings. The second feature of the article, and one that will re-emerge from time to time in the discussion, is the correction of misinterpretations and information given on *caernensis*.

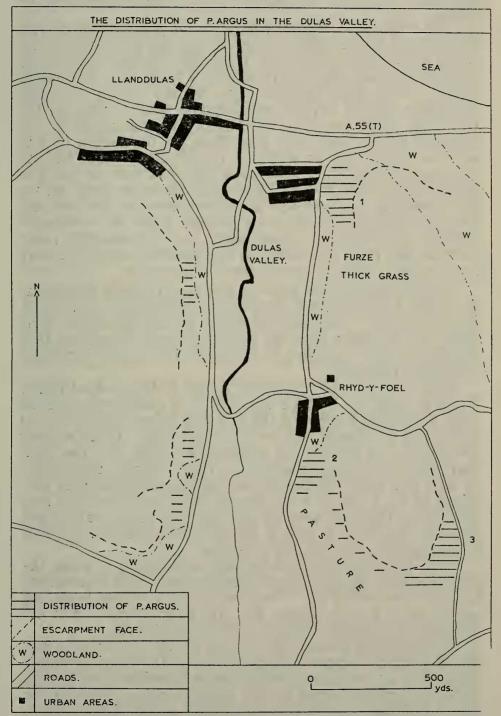
The Distribution of P. Argus caernensis Th.

The information available to most readers on this subject is contained in Ford's 'Butterflies'. He was provided with this information by J. A. Thompson, and the latter has of him-

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self written a short paper on the subject. Yet the data contained in Ford's volume is surprisingly misleading:—

"P. argus caernensis is to be found at a considerable elevation on limestone cliffs at several places on the north coast of Caernarvon" (Ford 1945, 1957, 296).



It is in fact only to be found on the Gt. Orme and in the Dulas Valley at Rhyd-y-Foel. G. Ellis (1949) did report (presumably from his own records) an occurrence of the race on the Creuddyn limestone at Pabo; this however indicates on the absence of Gloddaeth records, that dispersal from the Gt. Orme had miraculously avoided the most northerly limestone ridge on the Creuddyn, that adjacent to the Gt. Orme, or that the insect had been extinguished there prior to his observations.

The 1940's represented an exceptional period in every way. Comparison of the writer's records over the past 4 years with those of G. Ellis and earlier recorders indicates that many species once seen on the Creuddyn are no longer to be found there. It is quite possible that in this period P. argus caernensis spread beyond its markedly limited zone on the Gt. Orme. Even now in a period of climatic deterioration, the numbers of the insect are prodigious, to the extent that in some areas on the Gt. Orme it is difficult to walk without stepping on them; J. A. Thompson describes them as being in proliferation in the 1940's. This means that with every chance of favourable anemochore dispersal provided by constant north-westerly winds and gales in June, some of the number exposed to occasional displacement, and presumably many must be lost from the colony in this manner, could well have reached and colonized the Creuddyn Peninsular.

It must, however, be stressed that the Creuddyn Peninsular is neither a distributional zone for the subspecies, nor its location of origin. Constant surveying of the limestone areas along the N. Wales coast by the writer has shown that it is absent from the Creuddyn to Prestatyn, but for the important Rhyd-y-Foel colonies.

Its presence on the limestone slopes at Rhyd-y-Foel (maps 3 and 4 antea pp. 5 and 6 and Fig. 1) is easily explained. In 1952, Thompson mentioned the fact that he and Merchant had introduced *P. argus* to the Dulas Valley in 1948. Yet he neither mentioned the balance of numbers involved nor the location of this artificial introduction. (It is of crucial importance to have this data.) However, the current distribution is contained in fig. 1 (1971), and indicates that the species has now established three colonies on the east side of the valley, and that on the western side it has a more continuous spatial setting, yet its numbers are always low.

It is, of course, of much greater importance to know the exact confines of the insect's distribution. This information has been covered in fig. 1 here, and in fig 1 of the preceding article on *E. semele thyone* Th. Yet this information is not particularly valuable without environmental data.

A remarkable feature of the race on the Gt. Orme is contained in the widespread distribution of *H. nummularium* which is to be found everywhere on the headland but for the enclosed farmland areas on the summit table area—and the narrowly defined distributional zone of *P. argus* on the western side, with smaller colonies to the south. It is obvious, then, that the insect does not occupy the total area provided by the foodplant, and that other factors limit its distribution. It vertical extent on the headland is equally revealing. In the quotation given above, E. B. Ford gives the impression that the species is only found at considerable elevation on the Gt. Orme. In fact, it is found along the total length of the Marine drive from 20 ft. above O.D. through the contours to well over 400 ft., and its abundance at these elevations is only affected by the spatial magnitude of habitats provided for it. It is not the difference in altitude on the Gt. Orme that controls *argus* distribution, but the alterations in topography, and dependent factors. The actual confinement of the subspecies is contained within shallow, well-vegetated recesses on the limestone slopes, below the sheer escarpment faces. On more exposed slopes bounding the hollows, and on thinly vegetated slopes towards the summit in the absence of rock outcrops, population density is reduced markedly, and finally to zero.

In many ways, similar optimum conditions for the subspecies appear to present themselves on the east side of the Gt. Orme, yet the grass cover is generally thinner, and the only cover provided is bracken and a thick crop of dwarf furze. On the west side, the subspecies avoids the areas of furze, where the vegetation is presumably too dense for H. nummularium; yet it has a strong preference for the path along which the telegraph poles have been placed, and along similar stretches where cover is provided in clusters of fern, rubus ssp., juniper and Cotoneaster, and where the grass is thicker, and H. nummularium in greater density. During cloudy weather they become lost within this vegetative blanket. The restricted colonies at Rhyd-y-Foel are easily explained in terms of breaks effected by grazing (between Colonies 2 and 3), thick vegetation (between Colonies 1 and 2), and at high elevation above the escarpment faces where vegetation becomes extremely thin. The colonies in the Dulas Valley are neither large in areal extent, nor in terms of population numbers. As the insects, especially the males, are so evident while resting on the vegetation, it may well be presumed that insectivorous birds, of which there are many in the Dulas Valley, select heavily upon the species there. The differences between the Dulas Valley and Gt. Orme localities can perhaps be gauged from the alterations in frequency of certain morphological facets over the past 23 years. In this way the two populations perhaps act as indicators of different selective pressures.

It must perhaps be asked how unusual this environment is for *P. argus.* Elsewhere in N. Wales it was known on sandhills in the Lleyn Peninsular (Abersoch. G. Smith 1949) and on heathland in Anglesey (Trearddur Bay 1971). The Baron de Worms (1949) has indicated its eurytopism well enough:—

"In this country *Plebejus argus* affects large heathy tracts, mosses in the North, downlands, chalk cliffs, limestone cliffs, and even sandhills. Of these types of terrain it produces several local forms and many more abroad".

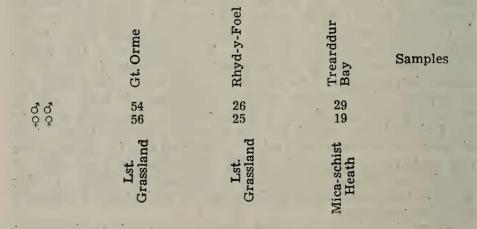
Its calcareous environment is then not so unusual. In

Kent, f. *cretacea*, and in Hampshire a downland population, both occupy chalk areas. It may well be that *P. argus* is then not only eurecious but also euryphagous, and this is adequately displayed in the lists of foodplants provided for it by many authorities. One feature is certain, and that is the ability of the species to occupy totally different environments and to produce local races. This is explained by the isolation of the colonies and the adaptability and variability of the species' gene pool.

The Morphocriteria of the Micro-geographical race caernensis Th. Samples.

Over the past three years, the writer has extracted a sample of *argus* from the Gt. Orme. The method of doing this is contained in the previous article on *E. semele thyone* Th. The means for various features were calculated for each annual sample, and very little variation was obtained between the individual samples, indicating that the phena were stabilized over that period.

During the last two weeks in June this year, a sample was taken from Rhyd-y-Foel Colony 1, perhaps the site of the artificial introduction in 1948. Also on the 20th July this year, as a measure of comparison, a sample of *P. argus* was acquired from Trearddur Bay near Holyhead, Anglesey; in the following discussion it must be continually borne in mind that this sample is the product of a day's sampling alone, and that this may well affect the statistical tests. The total area of each colony was covered by continual transects.



Features

The main aspects of the race are well known. The butterfly merges earlier than P. argus elsewhere, very often before E. semele thyone Th., and it is again a dwarfed race.

E. B. Ford has indicated that the males are pale blue and their black marginal borders are much reduced. "The females are always marked with blue", and "The orange lunules are inconspicuous or absent, never well developed".

Emergence date.—The race caernensis Th. is often on the wing in the second week of June, and certainly in full numbers by the 15th June. Its flight period is often considerably protracted, and the writer has seen it though in a somewhat pitiful condition, in early August (1970). In the Dulas Valley, the insect emerges slightly later than on the Gt. Orme; for instance this year P. argus was out on the Gt. Orme before the 15th June, and the females were on the wing, though in smaller numbers on the 18th June. In the Dulas Valley at Colony 1, on the 17th June, the males were just in the process of emerging and a single female was noticed by Mr J. Richens on the 20th June. Also the flight period comes to an earlier halt in the Dulas Valley, being at an end on the 17th July. P. argus at Treaddur is a July butterfly, and is separated temporally from the race *caernensis* perhaps in a similar way that thyone Th. is segregated from nomino-typical semele.

Size.—As measurements here follow the procedure described in an earlier article on *thyone* Th., no comparison can be easily made with figures given by E. B. Ford. The means of the various populations are given below:—

	Gt. Orme	Rhyd-y-Foel	Trearddur Bay	Wing expanse
ဝီ ဝီ	$\begin{array}{c} 27.6\\ 26.3\end{array}$	28·8	29·1	min.
ဝ္ ဝ္		27·2	27·9	mm.

Various tests were applied and indicvated the following relationship:

Gt. Orme v Trearddur Bay. $\int \int \chi^2(3)$ 12.54. P<0.01>0.001. Significant.

Gt. Orme v Rhyd-y-Foel. $\Im \Im \chi^2{}_{(3)}$ 7.0. P<0.1>0.05. Not significant. Gt. Orme v Rhyd-y-Foel. $\Im \Im \chi^2{}_{(2)}$ 3.37. P>0.1. Not significant.

(The Trearddur female sample was too small to apply a chi test.)

Certainly, the test would indicate that caernensis is significantly smaller than *argus* elsewhere, exemplified in this case by the Trearddur population. Yet it is not separated to a significant level from its related population in the Dulas Valley. Though the Rhyd-y-Foel figures are not perhaps large enough, nor have been collected over several years, yet a shift in the mean size of this population from typical *caernensis* is suggested by the actual figures themselves, and by the statistical tests; though on the other hand the difference may be no greater than that controlled by chance.

Markings and coloration.—It is not proposed to give a detailed analysis of these *P. argus* populations here; yet certain distinctive features can well be appreciated.

It is difficult to express the difference that exists in the

coloration of blue in the males between the *caernensis* and Trearddur series, except to confirm this without a subjective assessment; in the same way it may be added that the black border certainly appears to be reduced in *caernensis* specimens.

Some real differences can however actually be expressed objectively:—

 $\varphi \varphi$ —Orange lunules HM. UP., sub-marginal. It was mentioned above that E. B. Ford described the absence of the spots as one of the conspicuous features of the race *caernensis*. If indeed this was so in the 1940's, a marked change has occurred in the population both on the Gt. Orme and in the Dulas Valley. The means are given below:—

 $\Im \$ -Gt. Orme 4.8; Rhyd-y-Foel 4.2; Trearddur Bay 3.05 (the orange lunules of the Trearddur series are a redder orange).

They indicate to the contrary that the orange lunules are perhaps a central feature of the race; and this is amply displayed in the results given below:—

Gt. Orme v Rhyd-y-Foel $\Im \ \varphi \ \chi^{2}{}_{(2)}$ 7.9. P<0.05>0.01.

Gt. Orme v Trearddur $\Im \Im \chi^2_{(2)}$ 12.54. P<0.01>0.001.

As the writer would not question J. A. Thompson's assessment of the race, nor the information that he supplied to E. B. Ford, the above can have only one indication. This case exemplifies the nature of a complete shift in genetic frequencies; one that is probably related to current selective pressures operating within the maximum limits of a span of thirty years or so. It will be of great interest to follow this situation, and to see whether it is connected to a temporary period of variability (as those of *E. aurinia* described by E. B. Ford 1964) or to a new level of stability, and one of greater permanence.

 $\circ \circ$ Extension of violet on FW. UP. As a final comparison here—though there are additional features that can be assessed—nominal data of the extension of the blue area on the FW. UP. of the females can be tabulated in the manner shown below:—

Trearddur Bay Orme Gt. 7 None 4 21 11 Discal confinement 1 Discal and marginal zones 5 6 0 Extensive coverage

A glance at the figures will reveal an immediate asymmetry in a comparison of the data sets; but it also indicates that the amount of blue on UP of *caernensis* is perhaps not as great as is often assumed. A corollary of this may be included here. Whereas the area not covered by blue scales on the *caernensis* upperside tends towards a black-brown coloration, the Trearddur equivalent is a more true brown.

Overlap Characteristics, Population Changes and a Historical Reconstruction

There are two reasons for the above discussion. The first is to illustrate that the somewhat different habitat of *caernensis* is not as unusual as some authorities (B. P. Beirne, 1947) have assumed; that its fixation on the limestone headland and its choice of foodplant is perhaps well within current adaptability, negating Beirne's suggestions of glacial refugium in N. Wales.

Secondly, the overlap characteristics and population changes both on the Gt. Orme and in the Dulas Valley experiment, illustrate that not one of the discriminate features separating *caernensis* from *argus* populations is entirely successful. A dispersion diagram of the flight period and morphological characteristics would display a marked overlap of *caernensis* with the nominotypical populations (even in the absence of contiguous *argus* populations). Certainly *caernensis* may appear somewhat more unusual than other *argus* races, but it must be borne in mind that it and ssp. *masseyi* (Westmorland) are at the northerly limit of their range in Britain, and are very likely under more severe selective pressures.

In view of Weichselian geomorphological data briefly given in the previous article on *thyone* Th., and in respect of the thermal limits of *P. argus* in Britain and Scandinavia (South of July \pm 59°F), B. P. Beirne's suggestion of isolation and formation of this race on the headland during the Upper Pleniglacial is totally unrealistic.

It is more likely that arboreal confinement in one of the drier periods of the Flandrian (Boreal; Sub-Boreal) forced an *argus* population probably existing on the dune areas or *Ericaceae* covered boulder clay zones below the Gt. Orme, on to the limestone Headland, where it was well able to adapt itself to the hardy foodplant *H. nummularium*-characteristic of open places; ecological bounds well within the eurytopism of the species. It is likely that in this drier period, the Gt. Orme was desiccated to a greater extent than is at present usual; even in June (1970/71), the grass takes on a parched brown appearance. In the Boreal or Sub-Boreal drier climatic conditions, the insect may have been selected for rapid ontogeny in the manner described for *thyone* Th. Yet the difference cannot be great, since even in the absence of contiguous populations, the marked overlap of characteristics

with usual *argus* populations is indicative of the few factors involved, perhaps a single gene as E. B. Ford suggested.

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Why do Craneflies have Long Legs?

By ALAN E. STUBBS

Taxonomically one may regard Craneflies (Tipulidae) as primitive diptera, but in many respects they are quite advanced and their wide range of ecological adaptation and abundance shows them to be a successful group of insects. But one of the oddities about Craneflies is their long legs, surely not a 'primitive' character, which seem so cumbersome yet must have an advantageous role in the life of the adult cranefly.

Craneflies belong to the group of diptera called Nematocera and it may be as well to review the length of legs found in the various families. Craneflies consist of the large family Tipulidae, plus the small families Trichoceridae, Anisopidae and Ptychopteridae, but for the purposes of the main discussion, only Tipulidae are considered, since information is They are all elongate sparse on the other small families. insects with relatively long wings, though Anisopidae contains more robust insects with relatively shorter legs. Among other Nematocera, the Culicidae (mosquitoes), Cecidomyiidae and Chironomidae have fairly long legs. In the latter family the forelegs are often particularly long, suggesting an adaptive role, but in the small dumpy species, such as Cricotopus females the legs are correspondingly shorter. A similar situation is found in Ceratopogonidae where the squat biting species have short legs. Simulidae are short dumpy flies with short legs and broad short wings and Psychodidae fit into a similar pattern though less robust. The Mycetophilidae are a very varied group with some species not fitting the above pattern.

As a gross generalisation the picture emerges that long legs seem to be found when the insect is elongate and often the wings are also relatively elongate and narrow.

In some other groups of diptera, for instance *Leptogaster* (Asilidae) and *Baccha* (Syrphidae), there are elongate insects without unduly long legs (both examples are capable of hovering flight, unlike the Craneflies), so the Nematocera probably